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Male-biased night foraging by bumblebees (Hymenoptera, Apidae, *Bombus* spp.) in Taiwan

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Abstract

Known nocturnal behaviors of bees in the superfamily Apoidea, including the genus *Bombus*, were almost exclusively of females. Here we report observations of active free-ranging male *Bombus* at night in the plant nursery of the Fushan Research Center, Taiwan, in April 2022. Nectar feeding by males at inflorescences was confirmed by tongue-licking in the absence of pollen collecting. The numbers of active female and male bumblebees during the daytime were close to equal. In contrast, only males were found to be active in the night. Our observations suggest that such nocturnal activity is facultative. This finding not only provides a rare case of nocturnal activity in free-ranging *Bombus*, but also demonstrates that such behaviors can vary between the sexes.

Keywords

Bombus flavescens, nocturnal behavior, sex-biased

Circadian rhythm represents a key mechanism regulating temporal patterns of activity and physiological processes in animals. Given species tend to be diurnal, nocturnal or crepuscular, depending on whether their main active times are during daylight hours, at night or in twilight. The timing of daily activity may involve distinct selection forces on account of

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light conditions, weather, the distribution of important resources, and predation risk. Furthermore, synchronization with conspecifics of daily activity may be important in social and reproductive interactions (Sullivan 1981; Frisch and Koeniger 1994). On the other hand, asynchronization of daily activity among conspecifics could favor individuals via avoidance of severe intraspecific competition for critical resources (Alanärä et al. 2001).

Bumblebees (Hymenoptera; Apidae; *Bombus*) are a group of large social bees. The genus is most abundant in the northern hemisphere, where it provides critical pollination services to many crops and wild plants (Prys-Jones and Corbet 2011). While observations to date show both sexes to be active mainly or exclusively in the daytime, Chittka et al. (1999) recorded nocturnal feeding by *B. impatiens* workers in captive condition. Here we report observations of nocturnal activity in free-ranging male *Bombus* from northeastern Taiwan.

The observations were mainly made at the plant nursery of Fushan Research Center (24.7556°N, 121.5959°E) in Yilan County, Taiwan, from early to mid-April 2022. The climate is characterized by a strong seasonality that is mainly driven by the northeast monsoon in the winter and occasional typhoons in the late summer and early fall. The weather is generally mild and humid with a mean annual temperature of 18.2 °C and precipitation of 3,888 mm (Tu et al. 2023). The surrounding vegetation is primarily submontane evergreen broadleaf forest (Su et al. 2010). The plant nursery was established by Taiwan Forestry Research Institute (T.F.R.I.) to conserve endemic and threatened native plants. Since the observation area in the plant nursery had no insect exclusion nets, bumblebees can access the plants freely. An additional 1.6-km transect line was set along a trail of the nearby Fushan Botanical Garden in the later phase of the study, when many dicot plants were in bloom.

Bees' nocturnal behavior was initially noted by direct visual observation with lights from torch and headlamp. Later we utilized a night-vision video cam recorder (Canon XA40, Japan) with an 850 nm infrared torch (Nightfox NB5, U.K.) in order to record nocturnal activity without presenting a visual light stimulus. Bees found to be walking, flying, wing fluttering, or showing leg movements or nectar feeding were considered active. Nectar feeding is evidenced by extension of the tongues and licking movements at flowers, along with the absence of pollen-collecting movements.

Three bumblebee species have been reported from the Fushan area: *B. bicoloratus*, *B. eximius*, and *B. flavescens* (S.S.L., Y.C.H., and W.C.Y. unpublished data). We identified bees to species according to a key of the three species (Suppl. material 1) based on Starr (1992). However, the diagnostic traits to distinguish *B. eximius* and *B. flavescens* cannot be applied with confidence to active individuals, so that the two species are combined in our data as *B. eximius*/*B. flavescens*.

Six male bumblebees were spotted in active status on *Ligustrum pricei* during a night walk in the plant nursery between 20:50 and 21:00 on April 5th, 2022. All active bumblebees walked slowly among the branches and inflorescences and inspected both opened and unopened flowers during most of the observation time. One individual flew with wings slowly fluttering, from *L. pricei* to a neighboring plant. While the bees were in contact with stigma and pistil, they often extended their tongues in the typical nectar licking behavior (Fig. 1). No pollen collection actions were performed by the bees, consistent with feeding on nectar.

Additional observations of *B. eximius*/*B. flavescens* were made at the plant nursery and botanical garden (Table 1). While active bumblebees of both sexes had been seen at both sites in the daytime, nocturnal foraging behavior was again recorded solely from male bumblebees at the plant nursery (Suppl. material 2). No active females were observed in the three additional survey nights, but one inactive worker was recorded with two males on *Ajuga dictyocarpa*. In the only daytime observation, we recorded a similar number of male and worker *B. eximius*/*B. flavescens*, feeding at *L. pricei* and *A. dictyocarpa*.

Diurnality is considered the predominant habit in bees. Nocturnal and crepuscular activities have been reported from several genera of Apidae and Halictidae, including *Apis*, *Bombus*, *Lasioglossum*, *Megalopta* and *Xylocopa*, but exclusively from females (Chittka et al. 1999; Burgett and Sukumalanand 2000; Wcislo et al. 2004; Kelber et al. 2006; Tierney et al. 2008; Young et al. 2021). Our observation of facultative nocturnal foraging by *B. eximius*/*B. flavescens* provides a case of male bees showing considerable plasticity in daily activity pattern.

Night light has been suggested as a critical environmental factor driving nocturnal activities in bees (Kelber et al. 2006; Warrant 2008). In our case, the *B. eximius*/*B. flavescens* in Fushan were attracted by and licked unopened flowers of *L. pricei* (Suppl.

Figure 1. A male bumblebee at *Ligustrum pricei* flowers at night.

Table 1. Numbers of active and inactive *B. eximius/B. flavescens* individuals of each sex in each survey. Two males (FACT-00215031, FACT-00215032) identified as *B. flavescens* were deposited at the Forest Arthropod Collection of Taiwan (F.A.C.T.) in T.F.R.I. This survey session included both at the botanical garden and the plant nursery.

Date	Active bees	Inactive bees
2022 April 5th – night	6♂♂	–
2022 April 6th – night	–	–
2022 April 14th – day	12♂♂, 10♀♀	–
2022 April 14th – night	2♂♂	1♂, 1♀
2022 April 16th – night	–	7 (unknown sex)

material 3) and the white flower tags that we labeled on the tree several times. The misrecognition suggests that the bees used visual cues when targeting food resources. However, the two nights when active bees were observed were cloudy and dark, suggesting that *B. eximius/B. flavescens* may also use chemical cues for foraging in addition to vision (Chittka et al. 1999; Kulahci et al. 2008; Lawson et al. 2018).

Studies have shown that consumption of nutrient supplements could increase low temperature tolerance and survivorship from acute cold (Owen et al. 2013; Abou-Shaara 2017). In the low elevation mountainous areas (<1000 m a.s.l.) of Taiwan, male bumblebees, especially *B. flavescens*, emerge in spring (Sung et al. 2011). Unlike the females feeding on nectar and collecting pollen, male bumblebees were found feeding exclusively on nectar. They feed in the day and usually stay on inflorescences in the night (Prys-Jones and Corbet 2011). Both *Ligustrum pricei* and *Ajuga dictyocarpa* blossom in the day, and their flowers last for around 24 hours. Nectar-feeding behaviors in bumblebees suggest that the nectar is available throughout the day.

On the other hand, only half of the surveyed nights showed male bumblebees on plants. During the study period, bumblebees reduced their nocturnal activity when the wind became stronger and temperature dropped, becoming active again when the wind speed lowered. It might be too energetically costly for the bees to remain active during bad weather conditions.

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Supplementary material 1

Identification keys to bumblebee species of the Fushan area

Authors: Yun-Chen Hsieh, Joe Chun-Chia Huang

Data type: docx

Link: https://doi.org/10.3897/jhr.96.113486.suppl1

Supplementary material 2

Behavior of a male bumblebee on the inflorescences of *Ligustrum pricei* at night

Authors: Joe Chun-Chia Huang

Data type: mov

Link: https://doi.org/10.3897/jhr.96.113486.suppl2

Supplementary material 3

A bumblebee worker licking unopened flowers of *Ligustrum pricei*

Authors: Joe Chun-Chia Huang

Data type: mov

Link: https://doi.org/10.3897/jhr.96.113486.suppl3